Zoosyst. Evol. 102 (1) 2026, 285–302 | DOI 10.3897/zse.102.178601

A new species of the genus *Trimeresurus* Lacépède, 1804 (Squamata, Viperidae) from western Sichuan Province, China

Bo Cai[1], Yubo Gou[2,3], Gang Wang[4], Fengjing Liu[5], Dong Liang[6], Xiaodong Gu[7], Haijun Gu[8], Haolong Fang[9], Yuzhou Liu[10], Qiujie Li[2,11], Li Ding[1]

1 *Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610213, Sichuan, China*
2 *Giant Panda National Park Chengdu Administration, Chengdu 610000, Sichuan, China*
3 *Chengdu Botanical Garden, Chengdu Park City Botanical Science Research Institute, Chengdu 610000, Sichuan, China*
4 *College of Chemistry and Life Sciences / Sichuan Provincial Forestry and Grassland Key Laboratory of Biodiversity Conservation and Sustainable Community Development in Giant Panda National Park, Chengdu Normal University, Chengdu 611130, Sichuan, China*
5 *Jiangsu Key Laboratory for the Biodiversity Conservation and Sustainable Utilization in the Middle and Lower Reaches of the Yangtze River Basin, College of Life Sciences, Nanjing Normal University, Nanjing 210023, Jiangsu, China*
6 *Sichuan Mt. Emei Forest Ecosystem National Observation and Research Station / Institute of Mount Emei World Cultural and Natural Heritage, Mount Emei Scenic Area Management Committee, Emeishan 614201, Sichuan, China*
7 *Department of Nature Reserves, Sichuan Forestry and Grassland Bureau, Chengdu 610081, Sichuan, China*
8 *General Station for Nature Reserve Management, Sichuan Forestry and Grassland Bureau, Chengdu 610081, Sichuan, China*
9 *School of Applied Technology, Southwest University of Science and Technology, Mianyang 621000, Sichuan, China*
10 *Design College, Shandong University of Arts, Ji'nan 250300, Shandong, China*
11 *Chengdu Academy of Agriculture and Forestry Sciences, Chengdu 610000, Sichuan, China*

https://zoobank.org/94F11312-2842-4408-9102-EDBAD8F660E7

Corresponding author: Li Ding (dingli@cib.ac.cn)

Academic editor: Justin Bernstein ♦ **Received** 29 November 2025 ♦ **Accepted** 11 January 2026 ♦ **Published** 30 January 2026

Abstract

The genus *Trimeresurus* Lacépède comprises over 57 species, with recent taxonomic revisions recognizing six subgenera. Despite extensive research, many regions in China remain understudied, particularly the biodiversity-rich West China Rain Zone. This study reports a new pitviper species from western Sichuan Province, China, based on comprehensive morphological and molecular analyses. Specimens collected from the West China Rain Zone were examined using detailed morphological comparisons and phylogenetic analyses of three mitochondrial genes (*16S*, *cytb*, and *ND4*). The results show that this population, together with *T. loong*, forms a distinct monophyletic clade within the subgenus *Viridovipera* Malhotra & Thorpe, with uncorrected genetic distances to its closest relatives exceeding 6.50% (*cytb*) and 5.77% (*ND4*). Diagnostic morphological differences, including smooth cephalic scales, a postocular streak extending beyond the 2nd supralabial in males, dorsal scale rows of 21–21–15, and a grass-green body color lacking bands or markings, further support its taxonomic distinctness. We propose the new species *Trimeresurus lii* **sp. nov.**, which represents the second species of *Viridovipera* in Sichuan Province and the 58th species of *Trimeresurus* worldwide, and contributes to understanding biodiversity in the Giant Panda National Park region. This discovery highlights the importance of continued field surveys in biodiversity hotspots for documenting and conserving unique faunal assemblages.

Key Words

Bamboo pitviper, biodiversity hotspots, Giant Panda National Park, morphology, snakebite envenoming, *Viridovipera*, West China Rain Zone

Copyright *Cai, B. et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The Asian pitvipers of the genus *Trimeresurus* Lacépède, 1804, represent a diverse group of venomous snakes comprising over 57 species, distributed throughout South and Southeast Asia and often sharing habitats with human settlements in mountainous regions (Liang et al. 2025; Uetz et al. 2025; Xu et al. 2025a, b). The phylogenetic relationships within this genus have been relatively well studied, revealing several distinct lineages; consequently, it has been proposed that the genus should be split into multiple genera (Malhotra and Thorpe 2004a; Guo and Wang 2011). Subsequently, considering the complexity of *Trimeresurus*, these genera were suggested to be retained as subgenera (David et al. 2011; Mirza et al. 2023): *Cryptelytrops* Cope, 1860; *Himalayophis* Malhotra & Thorpe, 2004; *Parias* Gray, 1849; *Popeia* Malhotra & Thorpe, 2004; *Sinovipera* Guo & Wang, 2011; *Trimeresurus*; and *Viridovipera* Malhotra & Thorpe, 2004.

Among them, the subgenus *Viridovipera* currently includes nine recognized species: *T. mayaae* Rathee, Purkayastha, Lalremsanga, Dalal, Biakzuala, Muansanga & Mirza, 2022; *T. medoensis* Zhao, 1977; *T. nujiang* Liang, Ding, Vogel, Chen & Wu, 2025; *T. loong* Xu, Deng, Zhang, Nguyen, Poyarkov, Vogel & Peng, 2025; *T. pretiosus* Xu, Nguyen, Wang, Zhang, Poyarkov, Wei, Vogel, Peng & Weng, 2025; *T. stejnegeri* Schmidt, 1925; *T. truongsonensis* Orlov, Ryabov, Bui & Ho, 2004; *T. vogeli* David, Vidal & Pauwels, 2001b; and *T. yunnanensis* Schmidt, 1925. Based on overlapping morphological characters and molecular data, Liang et al. (2025) synonymized *T. gumprechti* David et al., 2002, a former member of *Viridovipera*, with *T. yunnanensis*, thereby reducing the number of valid species in this subgenus.

Currently, 16 species of *Trimeresurus* have been recorded in China (Cai 2025; Liang et al. 2025; Xu et al. 2025a, b), with the majority distributed across southwestern, southern, and eastern regions. *T.* (*Viridovipera*) *stejnegeri* is the most widely distributed species of the genus *Trimeresurus* in China, ranging from Taiwan Island to Sichuan Province and extending to northern Vietnam (Guo et al. 2016).

In Sichuan Province, *Trimeresurus stejnegeri* is found in areas almost surrounding the Sichuan Basin (Zhao et al. 1998), and it is the only representative of the subgenus *Viridovipera* in Sichuan (Cai 2023). Guo et al. (2016) conducted a phylogeographic study based on 171 samples collected from 47 localities in China, including Taiwan Island. Their gene tree revealed two well-supported clades within *T. stejnegeri*, corresponding to southwestern and southeastern China, respectively, including eastern and southern regions of Sichuan Province. Notably, Guo et al. (2016) did not include any samples from western Sichuan Province. Populations of *Trimeresurus* in western Sichuan have historically been identified as *T. stejnegeri* based solely on morphological characteristics (Zhao et al. 1998). Consequently, the taxonomic status of western Sichuan populations remains unverified by molecular evidence to date.

During multiple herpetological diversity surveys from 2019 to 2025, we collected a series of *Trimeresurus* cf. *stejnegeri* specimens in western Sichuan. After detailed morphological comparisons and comprehensive molecular phylogenetic analyses, we conclude that this population represents an undescribed species.

Materials and methods

Sampling

Fieldwork was carried out in Sichuan Province by Bo Cai, Dong Liang, Yubo Gou, Fengjing Liu, Hao-long Fang, Yuzhou Liu, and Qiujie Li in 2019–2025, and by Gang Wang in 2021 (Fig. 1).

Live animals were photographed to document color patterns prior to euthanasia. Euthanasia was performed via intracolonic injection of 250 mg/kg of 1% MS–222 (Chengdu, China) for anesthesia, followed by intracolonic injection of 75% alcohol (Chengdu, China). Liver tissue samples were collected and stored in 95% ethanol for molecular analyses, and specimens were preserved in 75% ethanol. Specimens were deposited at the Museum of Herpetology, Chengdu Institute of Biology, Chinese Academy of Sciences (**CIB**), and the Laboratory of the College of Chemistry and Life Sciences, Chengdu Normal University (**CNU**).

All procedures followed the regulations of the Wildlife Protection Law of China and were approved by the Animal Ethics Committee of CIB (Protocol No. CIB20191288; ethical approval date: 7 March 2019).

Molecular and phylogenetic analysis

A total of 242 sequences were analyzed (Table 1), of which 20 were newly generated in this study and 222 were retrieved from GenBank and DDBJ. These sequences represent 36 species of *Trimeresurus* and two outgroup taxa, *Craspedocephalus puniceus* and *Peltopelor malabaricus*.

Total genomic DNA was extracted from ethanol-preserved liver tissues using the QIAamp DNA Mini Kit (QIAGEN, Changsheng Biotechnology Co., Ltd., Changchun, China). Samples were sequenced for three mitochondrial genes: *16S* ribosomal RNA (*16S*), *cytb*, and *ND4*. The primers used for *16S* were 16Sar–L (5'-CGCCTGTTTATCAAAAACAT-3') and 16Sbr–H (5'-CCGGTCTGAACTCAGATCACGT-3'), following Parkinson et al. (2000). The primers used for *cytb* were L14910 (5' – AACCACCGTTGTACATCAACT - 3') and H16064 (5' – CTTTGGCTTACAAGAACAATGCTTTA - 3') following Burbrink et al. (2000). The primers used for *ND4* were ND4 (5' – TGACTACCAAAAGCTCATGTAGAAGC - 3') and Leu (5' – TACTTTTACTTCGATTTGCACCA - 3') following Parkinson et al. (2000). PCR amplification and sequencing methods followed Chen et al. (2020). The acquired nucleotide sequences were initially subjected to forward- and reverse-strand

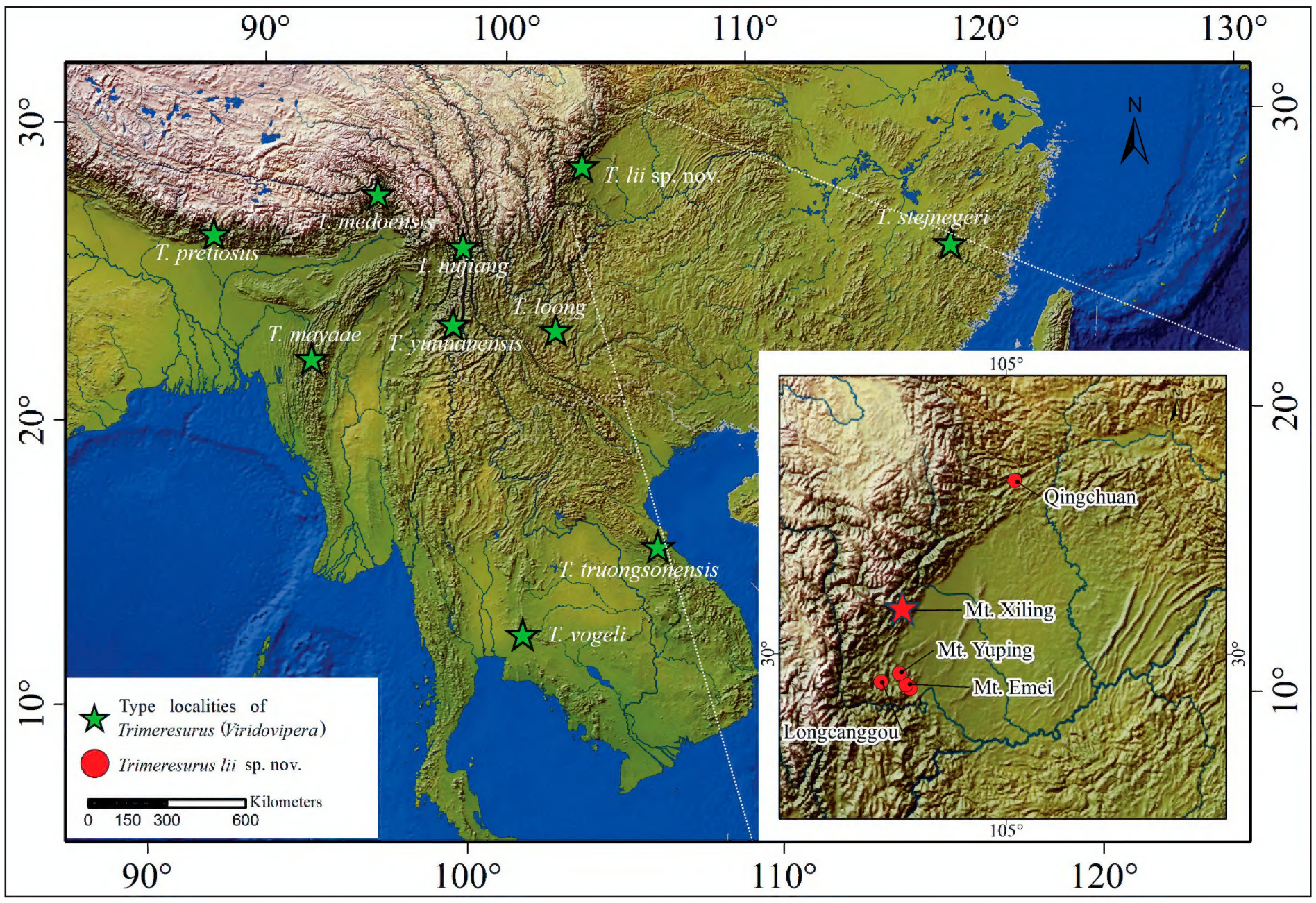

Figure 1. Map showing the type localities of *Trimeresurus* (*Viridovipera*) species and the localities of *Trimeresurus lii* sp. nov.

proofreading and editing using SeqMan (v7.1.0) in the DNAStar software package (v7.1; DNAStar Inc., Madison, WI, USA) (Skwor et al. 2012).

For phylogenetic analyses, homologous DNA sequences of related species were downloaded from GenBank and DDBJ and incorporated into subsequent analyses (Table 1). Sequences were aligned in PhyloSuite 1.2.3 (Zhang et al. 2020) using MAFFT (Katoh and Standley 2013) with default settings. Phylogenetic analyses were conducted using Bayesian inference (BI) and maximum likelihood (ML) methods implemented in MrBayes v3.2.7a (Ronquist et al. 2012) and IQ-TREE v2.2.0 (Nguyen et al. 2015), respectively. Prior to phylogenetic analyses, the best-fit evolutionary model was selected under the Bayesian information criterion (BIC) using PartitionFinder 2 (Lanfear et al. 2017). The GTR + F + I + G4 model was selected as the best model for all three fragments (*16S*, *cytb*, and *ND4*). In BI analyses, two runs were performed simultaneously with four Markov chains. The chains were run for 10,000,000 generations and sampled every 1000 generations. The first 25% of sampled trees were discarded as burn-in, and the remaining trees were used to estimate Bayesian posterior probabilities (BPPs). In ML analyses, 1000 bootstrap pseudoreplicates using the ultrafast bootstrap (UFB) approximation algorithm were conducted to construct the final consensus tree. Uncorrected genetic pairwise distances (*p*-distances) for *cytb* and *ND4* were calculated separately using default parameters in MEGA X (Kumar et al. 2018). Newly generated sequences were submitted to GenBase at the National Genomics Data Center (NGDC), Beijing Institute of Genomics, Chinese Academy of Sciences/China National Center for Bioinformation (Bu et al. 2024; CNCB-NGDC Members and Partners 2025) (Table 1).

Morphological comparison

Fifteen specimens of *Trimeresurus* cf. *stejnegeri* (11 males and four females) from western Sichuan were examined (Table 2). Data from published papers were also included in the study (Schmidt 1925, 1927; Maki 1931; Pope 1935; Zhao et al. 1998; David et al. 2001a, b, 2002; Ao et al. 2004; Orlov et al. 2004; David and Mathew 2005; Zhao 2006; Che et al. 2020; Rathee et al. 2022; Elangbam et al. 2023; Liang et al. 2025; Xu et al. 2025a, b). Morphological characters reported by David et al. (2001a, b), Zhao et al. (1998), and Xu et al. (2025b) were recorded as follows:

Measurements (adults only, snout–vent length and tail length to the nearest 1 mm using a steel ruler; other relatively short measurements [e.g., head width, eye diameter] to the nearest 0.1 mm using a digital caliper): snout to vent length (**SVL**): measured from the tip of the snout to the vent; tail length (**TAL**): measured from the vent to the tip of the tail; total length (**TL**): sum of snout–vent length and tail length; ratio of tail length to total length (**TAL/TL**); head length (**HL**): measured from the tip of the snout to the posterior margin of the mandible; head width (**HW**):

Table 1. NCBI/DDBJ/NGDC accession numbers for the sequences used in this study. * = DDBJ accession number; # = NGDC accession number.

NO.	Species Name	Locality	Voucher NO.	*16S*	cytb	*ND4*	References
Genus *Trimeresurus*							
Subgenus *Viridovipera*							
1	***T. lii* sp. nov.**	Mt. Xiling Snow Sichuan, China	CB249CD01	–	C_AA122992.1#	–	This study
	***T. lii* sp. nov.**	Xiling Snow Mountain, Sichuan, China	CB249CD03	–	C_AA122993.1#	–	This study
	***T. lii* sp. nov.**	Xiling Snow Mountain, Sichuan, China	CB249CD17	–	C_AA122994.1#	–	This study
	***T. lii* sp. nov.**	Emei Mountain, Sichuan, China	CB2105	C_AA122995.1#	C_AA122987.1#	C_AA123001.1#	This study
	***T. lii* sp. nov.**	Emei Mountain, Sichuan, China	CB2110	C_AA122996.1#	–	C_AA123002.1#	This study
	***T. lii* sp. nov.**	Emei Mountain, Sichuan, China	CB2119	C_AA122997.1#	C_AA122988.1#	C_AA123003.1#	This study
	***T. lii* sp. nov.**	Emei Mountain, Sichuan, China	CB2120	C_AA122998.1#	C_AA122989.1#	C_AA123004.1#	This study
	***T. lii* sp. nov.**	Yuping Mountain, Sichuan, China	CB2121	C_AA122999.1#	C_AA122990.1#	C_AA123005.1#	This study
	***T. lii* sp. nov.**	Emei Mountain, Sichuan, China	CB2127	C_AA123000.1#	C_AA122991.1#	C_AA123006.1#	This study
2	*T. loong*	Anning, Kunming, Yunnan, China	QHU R2025027	LC899328*	LC899334*	LC899341*	(Xu et al. 2025a)
	T. loong	Anning, Kunming, Yunnan, China	QHU R2025028	LC899329*	LC899335*	LC899342*	(Xu et al. 2025a)
	T. loong	Anning, Kunming, Yunnan, China	QHU R2025029	LC899330*	LC899336*	LC899343*	(Xu et al. 2025a)
	T. loong	Anning, Kunming, Yunnan, China	QHU R2025030	LC899331*	LC899337*	LC899344*	(Xu et al. 2025a)
	T. loong	Anning, Kunming, Yunnan, China	QHU R2025031	LC899332*	LC899338*	LC899345*	(Xu et al. 2025a)
	T. loong	Anning, Kunming, Yunnan, China	QHU R2025032	LC899333*	LC899339*	LC899346*	(Xu et al. 2025a)
3	*T. nujiang*	Gongshan, Yunnan, China	DL R353	PV994716	PX021391	PX021401	(Liang et al. 2025)
	T. nujiang	Gongshan, Yunnan, China	DL-03-622	PV994717	PX021392	PX021402	(Liang et al. 2025)
	T. nujiang	Gongshan, Yunnan, China	DL19	PV994718	PX021393	PX021403	(Liang et al. 2025)
	T. nujiang	Fugong, Yunnan, China	ANU ZR24133	PX061893	PX068374	PX094009	(Liang et al. 2025)
4	*T. pretiosus*	Yadong, Xizang, China	QHUR2025019	PX061894	PX068368	PX094011	(Xu et al. 2025b)
	T. pretiosus	Yadong, Xizang, China	QHUR2025020	PX061895	PX068369	PX094010	(Xu et al. 2025b)
	T. pretiosus	Yadong, Xizang, China	QHUR2025021	PX061895	PX068370	PX094012	(Xu et al. 2025b)
5	*T. yunnanensis*	Loei, Thailand	AM A164	AF517181	AY352766	AF517224	(Malhotra and Thorpe 2004a; Creer et al. 2003)
	T. yunnanensis	Pu Mat NP, Nghe An, Vietnam	AM B174	AY059563	AY059573	AY059595,	(Malhotra and Thorpe 2004b)
	T. yunnanensis	Jingdong, Yunnan, China	GP 851	–	KT216392	KT216441	(Guo et al. 2015)
	T. yunnanensis	Lincang, Yunnan, China	GP 3507	KT216339	KT216384	KT216433	(Guo et al. 2015)
	T. yunnanensis	Lincang, Yunnan, China	GP 3509	KT216341	KT216386	KT216435	(Guo et al. 2015)
	T. yunnanensis	Longling, Yunnan, China	KIZ 05089	KT216352	KT216399	KT216448	(Guo et al. 2015)
	T. yunnanensis	Jingdong, Yunnan, China	KIZ 047083	KT216351	KT216398	KT216447	(Guo et al. 2015)
	T. yunnanensis	Tengchong, Yunnan, China	QHU R2025033	LC899641*	LC899640*	LC899647*	(Xu et al. 2025b)
6	*T.* cf. *yunnanensis*	Honghe, Yunnan, China	GP 2532	KT216331	KT216376	KT216425	(Guo et al. 2015)
7	*T.* cf. *yunnanensis*	Pingbian, Yunnan, China	GP 3273	KT216334	KT216379	KT216428	(Guo et al. 2015)
	T. cf. *yunnanensis*	Pingbian, Yunnan, China	GP 3275	KT216336	KT216381	KT216430	(Guo et al. 2015)
	T. cf. *yunnanensis*	Mengzi, Yunnan, China	GP 3564	KT216344	KT216389	KT216438	(Guo et al. 2015)
	T. cf. *yunnanensis*	Mengzi, Yunnan, China	GP 3589	KT216345	KT216390	KT216439	(Guo et al. 2015)
	T. mayaae	Champhai, Mizoram, India	NCBS NRC-AA-0012	–	OM966859	–	(Rathee et al. 2022)
	T. mayaae	Ri-Bhoi, Meghalaya, India	BNHS 3658	–	OM966860	–	(Rathee et al. 2022)
	T. mayaae	Ri-Bhoi, Meghalaya, India	VR/ERS/ZSI/833	–	OM966862	–	(Rathee et al. 2022)
	T. mayaae	Kangpokpi, Manipur, India	MZMU 2970	–	OQ968476	–	(Elangbam et al. 2023)
8	*T. medoensis*	Motuo (Medog), Xizang, China	SYS r001831/CHS824	MK194252	MK201553	–	(Li et al. 2020)
	T. medoensis	Motuo (Medog), Xizang, China	KIZ YPX46122	MW020095	MW111479	–	(Che et al. 2020)
	T. medoensis	Motuo (Medog), Xizang, China	KIZ YPX46123	MW020331	MW133479	–	(Che et al. 2020)
	T. medoensis	Motuo (Medog), Xizang, China	ANU ZR24025	–	PX068371	PX094008	(Xu et al. 2025a)
	T. medoensis	Motuo (Medog), Xizang, China	ANU ZR24026	–	PX068372	PX094007	(Xu et al. 2025a)
	T. medoensis	Motuo (Medog), Xizang, China	ANU ZR24072	–	PX068373	–	(Xu et al. 2025b)
9	*T.* cf. *medoensis*	Kachin, Myanmar	AM B416/CAS 221528	AY352735	AY352765	AY352831	(Malhotra and Thorpe 2004a)
	T. cf. *medoensis*	Northeast India	V18	MG995794	MG995819	MG995834	Unpublished
10	*T. stejnegeri*	Mt. Wuyi, Fujian, China	GP 816	–	KX019140	KX019294	(Guo et al. 2016)
	T. stejnegeri	Mt. Jinggang, Jiangxi, China	GP 662	–	KX019120	KX019274	(Guo et al. 2016)
	T. stejnegeri	Qimen, Anhui, China	GP 470	–	KX019094	KX019248	(Guo et al. 2016)
	T. stejnegeri	Jinhua, Zhejiang, China	GP 633	–	KX019111	KX019265	(Guo et al. 2016)
	T. stejnegeri	Youxi, Fujian, China	GP 755	–	KX019131	KX019285	(Guo et al. 2016)

NO.	Species Name	Locality	Voucher NO.	*16S*	cytb	*ND4*	References
	T. stejnegeri	Dehua, Fujian, China	GP 2435	–	KX019054	KX019209	(Guo et al. 2016)
	T. stejnegeri	Taichung, Taiwan, China	AM TST23	–	AF277689	EU443799	(Creer et al. 2003; Dawson et al. 2008)
	T. stejnegeri	Mt. Diaoluo, Hainan, China	GP 45	–	KX019088	KX019242	(Guo et al. 2016)
	T. stejnegeri	Qiongzhong, Hainan, China	GP 46	–	KX019089	KX019243	(Guo et al. 2016)
	T. stejnegeri	Qiongzhong, Hainan, China	GP 48	–	KX019104	KX019258	(Guo et al. 2016)
	T. stejnegeri	Cat Ba NP, Hai Phong, Vietnam	GP 881	–	KX019145	KX019299	(Guo et al. 2016)
	T. stejnegeri	Phia Oac-Phia Den NP, Cao Bang, Vietnam	ROM 35321	–	KT216408	KT216457	(Guo et al. 2016)
	T. stejnegeri	Nonggang, Guangxi, China	GP 2461	–	KX019056	KX019211	(Guo et al. 2016)
	T. stejnegeri	Nanchuan, Chongqing, China	GP 1227	–	KX019007	KX019162	(Guo et al. 2016)
	T. stejnegeri	Leishan, Guizhou, China	GP 1887	–	KX019034	KX019189	(Guo et al. 2016)
	T. stejnegeri	Luoding, Guangdong, China	KIZ 09939	–	KX019158	KX019312	(Guo et al. 2016)
	T. stejnegeri	Enshi, Hubei, China	GP 2011	–	KX019040	KX019195	(Guo et al. 2016)
11	*T. truongsonensis*	Phong Nha-Ke Bang NP, Quang Binh, Vietnam	AM B659/VNUH 190606	EU443818	EU443815	EU443816	(Dawson et al. 2008)
	T. truongsonensis	Khammouane, Laos	ZMMU NAP-09115	–	PX068365	PX094015	(Xu et al. 2025b)
12	*T. vogeli*	Nakhon Ratchasima, Thailand	AM B97	AY059562	AY059574	AY059596	(Malhotra and Thorpe 2004a)
	T. vogeli	Nakhon Ratchasima, Thailand	ZMMU NAP-08227	–	PX068366	PX094013	(Xu et al. 2025b)
	T. vogeli	Nakhon Ratchasima, Thailand	ZMMU NAP-08228	–	PX068367	PX094014	(Xu et al. 2025b)
13	*T.*cf. *loong.*	Huili, Sichuan, China	GP 37	EU443812	EF597522	EF597527	(Dawson et al. 2008)
	*T.*cf. *loong.*	Huili, Sichuan, China	GP 38	EU443814	EF597523	EF597528	(Dawson et al. 2008)
Subgenus *Himalayophis*							
14	*T. arunachalensis*	Northeast India	APF/SFRI-1871	MK722155	MK720609	–	(Malhotra and Thorpe 2004a)
15	*T. tibetanus*	Nepal	AM B258	AY352715	AY352749	AY352810	(Malhotra and Thorpe 2004a)
Subgenus *Parias*							
16	*T. flavomaculatus*	Mindanao, Philippines	AM B4	AY352734	AY352764	AY352830	(Malhotra and Thorpe 2004a)
17	*T. hageni*	Songhkla, Thailand	AM B33	AY059552	AY059567	AY059585	(Malhotra and Thorpe 2004a)
18	*T. malcolmi*	Mt. Kinabalu, Sabah, Borneo, Malaysia	AM B349	AY371786	AY371832	AY371861	(Malhotra and Thorpe 2004a)
19	*T. mcgregori*	Bataan islands, Philippines	AM B289	AY371795	AY371831	AY371858	(Malhotra and Thorpe 2004a)
20	*T. schultzei*	Palawan, Philippines	AM B210	AY352725	AY352756	AY352819	(Malhotra and Thorpe 2004a)
21	*T. sumatranus*	Bengkulu, Sumatra, Indonesia	AM B367	AY371791	AY371824	AY371864	(Malhotra and Thorpe 2004a)
Subgenus *Sinovipera*							
22	*T. sichuanensis*	Sichuan, China	GP7/YBU030116	HQ850449	HQ850447	HQ850446	(Guo and Wang 2011)
Subgenus *Popeia*							
23	*T. lanna*	Doi Inthanon NP, Chiangmai, Thailand	AUP-00061	OR471637	OR470571	OR470534	(Idiiatullina et al. 2024b)
24	*T. nebularis*	Cameron Highlands, Pahang, Malaysia	AM B345	AY371775	AY371811	AY371849	(Sanders et al. 2006)
25	*T. phuketensis*	Phang Nga, Thailand	AM B467	AY371781	AY371807	AY371851	(Sanders et al. 2006)
26	*T. popeiorum*	Yingjiang, Yunnan, China	DL2017070101	MH779887	MH779875	MH779879	(Chen et al. 2019)
27	*T. sabahi sabahi*	Mt. Kinabalu, Sabah, Borneo, Malaysia	AM B344	AY371771	AY371815	AY371842	(Malhotra and Thorpe 2004a)
28	*T. tenasserimensis*	Suan Phueng, Ratchaburi, Thailand	ZMMU Re-17669	PP032802	OR999089	PP032781	(Idiiatullina et al. 2024b)
Subgenus *Trimeresurus*							
29	*T. albolabris*	Shek Kwu Chan, Hong Kong, China	AM A157	AY352744	AF171884	AY352839	(Malhotra and Thorpe 2000, 2004a)
30	*T. cantori*	Nicobar Is., India	AM A85	AY352741	AF171889	AY352836	(Malhotra and Thorpe 2000, 2004a)
31	*T. caudornatus*	Yingjiang, Yunnan, China	AR1238	MK575042	MK575036	MK575038	(Chen et al. 2020)
32	*T. ciliaris*	Thum Khao Ting, Trang, Thailand	ZMMU Re-17661	OR471621	OR470557	OR470538	(Idiiatullina et al. 2023)
33	*T. erythrochloris*	Tham Si Va Cave, Klong Hat, Sa Kaeo, Thailand	RIM-0079	PQ654052	PQ658816	PQ658818	(Pawangkhanant et al. 2025)
34	*T. erythrurus*	Rangoon, Myanmar	AM A209	AF517174	AF171900	AF517217	(Creer et al. 2003)
35	*T. kanburiensis*	Khao Yai NP, Kanchanaburi, Thailand	ZMMU Re-17667	–	OR470579	OR470553	(Idiiatullina et al. 2023; Idiiatullina et al. 2024a)
36	*T. macrops*	Bangkok, Thailand	ZMMU Re-17856	–	PP766219	PP779475	(Idiiatullina et al. 2024c)

NO.	Species Name	Locality	Voucher NO.	*16S*	cytb	*ND4*	References
Out group							
37	*Craspedocephalus puniceus*	Indonesia	AM B213	AF517177	AF517192	AF517220	(Creer et al. 2003)
38	*Peltopelor malabaricus*	Tamil Nadu, India	AM A218	AY059564	AY059569	AY059587	(Malhotra and Thorpe 2000, 2004a)

maximum head width; head height (**HH**): vertical height between dorsal and ventral surfaces of head, measured at HW; eye diameter (**ED**): horizontal diameter of the eye; nostril distance (**ND**); and interocular distance (**ID**).

Scale counts (adults only): preocular (**PRO**): number of scales touching prior side of the orbit; postocular (**PO**): number of scales touching posterior side of the orbit; interorbital scales (**IOS**), number of scales at the narrowest point between the orbits; supralabials (**SL**): scales behind the rostral shield and counted on upper lips; infralabials (**IL**): scales behind the mental shield and counted on lower lips; keeling of the temporal scales (KTEM); keeling of the occipital scales (KOCC); keeling of the cephalic scales (KCEP); dorsal scale rows (DSR): at one head length behind head (ASR), at midbody (MSR), and at one head length before vent (PSR); ventral scales (VEN): counted from the first ventral scale, which is wider than long, to the vent, excluding the cloacal plate; subcaudal scales (SC): number of subcaudal scales excluding the terminal scute; cloacal plate (CP).

Coloration was based on photographs of living and preserved specimens.

Results

Phylogenetic relationships

The BI and ML analyses produced similar phylogenetic tree topologies (Fig. 2), with all analyzed *Trimeresurus* species forming a strongly supported monophyletic group. In both phylogenetic reconstructions, the West China Rain Zone population and *T. loong* constitute a distinct monophyletic clade within the subgenus *Viridovipera*.

Mean uncorrected *p*-distances for the *cytb* and *ND4* genes of the studied *Viridovipera* species are summarized in Tables 3, 4, respectively. For the *cytb* gene, mean uncorrected *p*-distances ranged from approximately 4.47% (*T. mayaae* and *T.* cf. *medoensis*) and 5.13% (*T. mayaae* and *T. medoensis*) to 10.75% (*T. vogeli* and *T. pretiosus*) across all samples, whereas the genetic distance between the West China Rain Zone population and other congeners was at least 6.50% (vs. *T. loong*) (Table 3). For the *ND4* gene, mean uncorrected *p*-distances across all samples ranged from 4.01% (*T. yunnanensis* and *T.* cf. *yunnanensis*) and 4.58% (*T. stejnegeri* and *T. yunnanensis*) to 10.43% (*T.* cf. *medoensis* and *T. vogeli*), with the distance between the West China Rain Zone population and other congeners being at least 5.77% (compared with *T. loong*) (Table 4). These uncorrected *p*-distance results indicate that the West China Rain Zone population is genetically differentiated from other members of the subgenus *Viridovipera*. Based on its distinct phylogenetic placement, marked genetic differentiation, and consistent morphological distinctiveness, we describe this population as a new species and provide a formal description below.

Taxonomy

Trimeresurus lii **Cai, Liu, Liang, Wang & Ding, sp. nov.**

https://zoobank.org/60B2A6C5-8ADB-4561-8AF7-0B439EA575E7

Trimeresurus stejnegeri stejnegeri in west part of Sichuan. Zhao (2003).

Type materials. ***Holotype.*** • CIB 122871 (field number CB249CD017), adult male, collected from Xiling Town in Giant Panda National Park, Chengdu Area, Sichuan Province, China (30.68°N, 103.25°E; elevation 1,167 m a.s.l.), collected by the team of Bo Cai in 2025.

Paratypes (n = 14, all from Sichuan Province, China). • CIB 122872 (adult female, field number CB2119) and • CIB CB2110 (adult female), along with • CIB CB2105, • CIB CB2120, and • CIB CB2121 (adult males), collected from Emei Mountain Scenic Area in Emeishan City, Sichuan Province, China, by the team of Bo Cai in July 2021. • CNU 202109 (adult male) collected by the team of Gang Wang in September 2021. • CIB 83925 (field number 562142) and • CIB 13787 (field number 562141) (adult males), along with • CIB 13785 (field number 561785) and • CIB 13786 (field number 562191) (adult females), collected by Cheng-Chao Liu, Fuhua Liu et al. in 1956. • CIB 13772 (field number 639162), • CIB 13783 (field number 639163), and • CIB 13782 (field number 639246) (adult males) collected by Chenghan Liu in 1963. All these species are from Emei Mountain Scenic Area in Emeishan City. • CIB CB2127 adult male collected by the team of Bo Cai in September 2021 from Yuping Mountain Scenic Area in Hongya County, Meishan City.

Other types (n = 4, all from Sichuan Province, China). • CIB13775 (field number CIB561786, juvenile female), collected by Cheng-Chao Liu, Fuhua Liu et al. in 1956. • CIB CB249CD01 (subadult male), • CIB CB249CD02 (juvenile female), and • CIB CB249CD03 (juvenile male) were collected by Bo Cai's team during July–September 2024 and 2025 from the Xiling Snow Mountain Scenic Area in the Giant Panda National Park, Chengdu City.

Etymology. The specific epithet *lii* is a Latinized genitive form honoring LI Er (c. 6th–5th century BCE), traditionally revered as Laozi, the ancient Chinese philosopher whose teachings emphasize harmonious coexistence between humans and nature—a principle that aligns closely with the conservation ethos of the Giant Panda National Park, where this species was discovered. The known distribution of *Trimeresurus lii* sp. nov. in western

Table 2. Morphometric data (in mm) and meristic characters of the type series of *Trimeresurus lii* sp. nov.

Specimen Number	CIB 122871	CNU 202109	CIB CB2105	CIB CB2120	CIB CB2121	CIB CB2127	CIB 83925	CIB 13772	CIB 13787	CIB 13782	CIB 13783	CIB 122872	CIB CB2110	CIB 13785	CIB 13786
Type status	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Llocality	Mt. Xiling	Mt. Emei	Mt. Emei	Mt. Emei	Mt. Emei	Mt. Yuping	Mt. Emei	Mt. Emei	Mt. Emei	Mt. Emei	Mt. Emei	Mt. Emei	Mt. Emei	Mt. Xiling	Mt. Emei
Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀
SVL	457.0	515.1	643.0	568.0	532.0	553.0	675.0	585.0	598.0	586.0	490.0	795.0	518.4	425.0	635.0
TAL	110.0	127.9	146.0	152.0	131.0	172.0	176.0	120.0	169.0	174.0	125.0	136.0	93.6	104.0	166.0
TL	567.0	643.0	789.0	720.0	663.0	725.0	851.0	705.0	767.0	760.0	615.0	931.0	612.0	529.0	801.0
HL	24.5	26.9	32.3	33.6	24.9	30.5	29.5	26.0	31.9	34.3	26.4	41.5	25.2	26.2	36.8
HW	16.3	13.5	20.6	21.1	18.3	18.2	19.5	19.2	19.0	23.3	19.7	27.4	18.6	15.1	25.6
HH	8.8	8.4	12.9	12.1	11.1	10.9	11.5	10.2	14.7	11.9	9.9	16.1	10.3	9.3	14.8
ID	11.2	10.9	13.2	14.9	12.3	13.0	14.2	12.7	13.3	14.0	11.7	16.7	11.9	9.5	14.3
ND	4.0	4.7	6.0	5.6	4.8	5.2	6.2	5.9	6.5	6.6	6.5	6.1	4.7	3.5	6.7
ED	3.0	2.6	4.3	4.1	3.6	4.1	4.3	3.0	3.6	3.8	2.9	4.4	3.6	3.3	4.1
TaL/TL	0.194	0.199	0.185	0.211	0.198	0.237	0.207	0.170	0.220	0.229	0.203	0.146	0.153	0.197	0.207
TAL/SVL	0.241	0.248	0.227	0.268	0.246	0.311	0.261	0.205	0.283	0.297	0.255	0.171	0.181	0.245	0.261
HL/SVL	0.054	0.052	0.050	0.059	0.047	0.055	0.044	0.044	0.053	0.058	0.054	0.052	0.049	0.062	0.058
HW/SVL	0.036	0.026	0.032	0.037	0.034	0.033	0.029	0.033	0.032	0.040	0.040	0.034	0.036	0.035	0.040
HW/HL	0.080	0.502	0.636	0.629	0.734	0.598	0.662	0.737	0.595	0.680	0.747	0.660	0.740	0.575	0.697
ID/HL	0.457	0.406	0.409	0.442	0.493	0.426	0.480	0.490	0.418	0.407	0.442	0.403	0.471	0.361	0.388
ED/HL	0.122	0.098	0.132	0.123	0.144	0.134	0.145	0.115	0.111	0.111	0.111	0.105	0.145	0.126	0.112
VEN	154	163	160	164	165	163	163	167	152	160	164	160	163	163	168
SC	68	75	64	67	72	75	68	64	69	72	73	63	63	65	70
VEN+SC	222	238	224	231	237	238	231	231	221	232	237	223	226	228	238
DSR	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15	21-21-15
CP	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
SL	9/8	9/9	9/9	9/9	9/10	8/9	9/9	10/9	9/10	9/9	10/10	9/9	10/10	9/10	11/11
IL	12/11	11/11	11/11	12/12	10/10	10/10	12/11	11/10	11/12	12/12	10/11	11/11	11/11	12/13	12/12
CEP	10	11	12	11	12	11	10	11	11	10	13	11	10	11	12

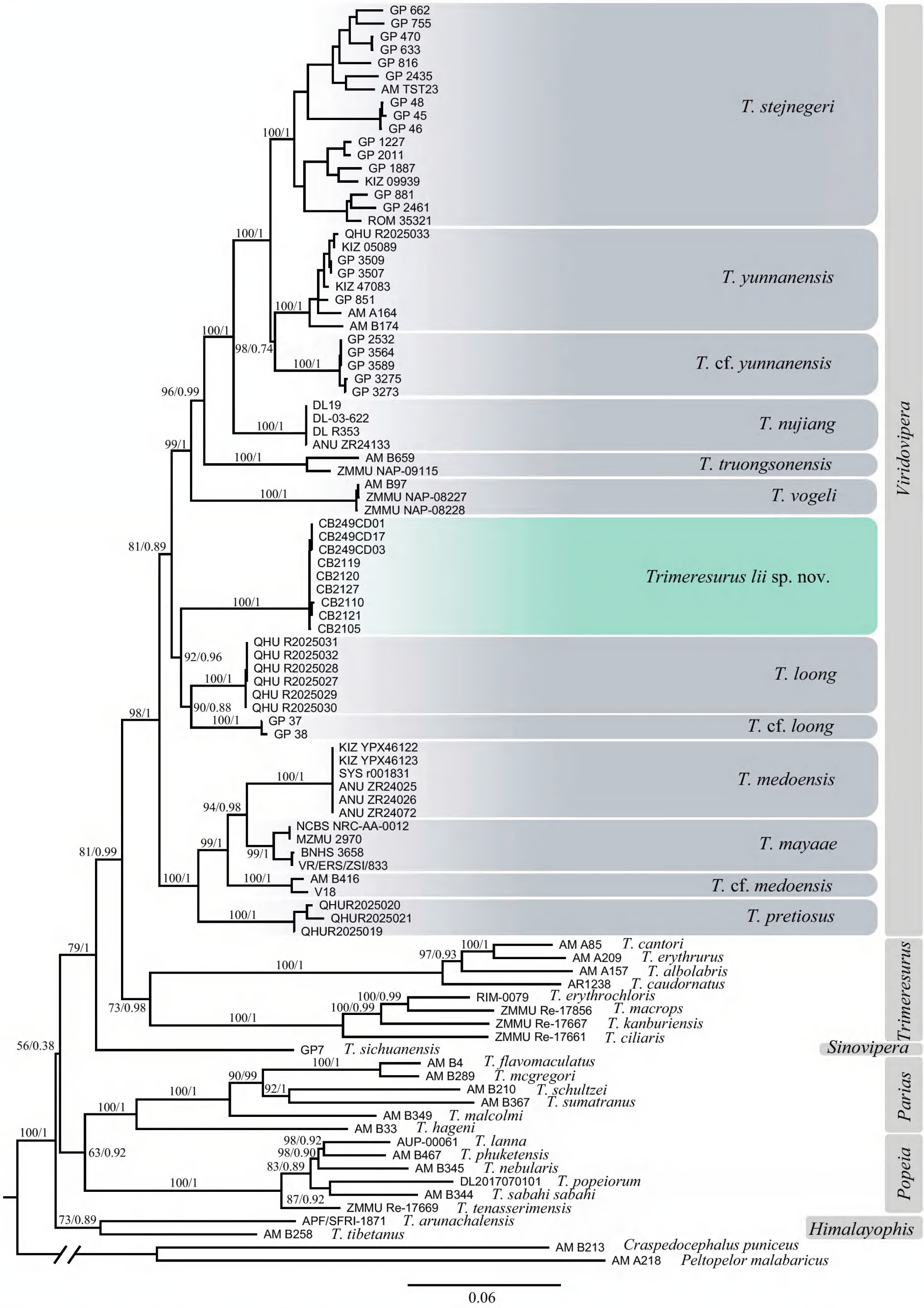

Figure 2. Maximum likelihood and Bayesian inference phylogenies based on three mitochondrial gene fragments (*16S*/*cytb*/*ND4*). Ultrafast bootstrap approximation (UFB) and Bayesian posterior probabilities (BPP) are denoted above each node.

Table 3. Uncorrected pairwise p-distances (%), representing the mean observed divergence, among subgenus *Viridovipera* species based on mitochondrial cytb gene sequences.

NO.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13
1	*Trimeresurus lii* sp. nov.													
2	*T. loong*	6.50												
3	*T.* cf. *loong*	6.75	4.60											
4	*T. yunnanensis*	8.52	8.17	8.87										
5	*T. nujiang*	7.25	6.97	7.11	5.82									
6	*T. stejnegeri*	8.95	8.20	8.35	5.88	6.71								
7	*T.* cf. *yunnanensis*	7.97	7.85	8.28	4.52	6.19	5.57							
8	*T. mayaae*	7.31	6.48	6.77	9.15	7.71	8.70	8.70						
9	*T.* cf. *medoensis*	6.63	6.47	6.76	8.90	6.95	8.26	7.78	4.47					
10	*T. medoensis*	8.35	7.52	8.14	9.72	8.23	8.85	9.49	5.13	6.49				
11	*T. truongsonensis*	8.73	7.88	7.88	8.07	7.49	8.15	7.73	8.32	8.14	9.26			
12	*T. vogeli*	9.38	7.55	8.58	9.89	8.17	9.53	9.85	8.81	8.61	9.33	9.24		
13	*T. pretiosus*	7.91	7.77	7.23	9.33	8.21	9.63	8.95	6.89	5.75	6.89	9.39	10.75	

Table 4. Uncorrected pairwise p-distances (%), representing the mean observed divergence, among subgenus *Viridovipera* species based on mitochondrial ND4 gene sequences.

NO.	Species	1	2	3	4	5	6	7	8	9	10	11	12
1	*Trimeresurus lii* sp. nov.												
2	*T. loong*	5.77											
3	*T.* cf. *loong*	5.72	4.46										
4	*T. yunnanensis*	7.53	6.41	6.39									
5	*T. nujiang*	8.04	5.86	6.35	5.05								
6	*T. stejnegeri*	7.51	6.76	6.80	4.58	6.14							
7	*T.* cf. *yunnanensis*	7.17	6.34	6.14	4.01	5.71	4.52						
8	*T.* cf. *medoensis*	8.01	7.59	6.71	8.95	8.23	8.45	7.90					
9	*T. medoensis*	7.27	7.68	7.43	8.40	8.66	8.06	7.58	6.25				
10	*T. truongsonensis*	6.86	6.24	6.67	7.58	7.39	7.66	7.25	8.02	8.97			
11	*T. vogeli*	7.20	6.53	7.41	7.61	7.80	7.71	8.22	10.43	9.08	7.37		
12	*T. pretiosus*	8.24	7.19	6.63	8.19	7.57	8.12	8.24	7.32	6.60	8.78	9.68	

Sichuan Province falls within the West China Rain Zone, a region historically associated with the early development of Daoist thought. In light of its geographic range and ecological context, we propose 'Huaxi Green Pitviper' as the English common name and '华西竹叶青蛇' (*Huáxī Zhúyèqīng Shé*) as the Chinese name.

Diagnosis (Table 2). This new species can be distinguished from all of its congeners by the following combination of morphological characters: (1) dorsal scale rows 21-21-15; (2) ventrals 152–167 in males and 160–168 in females; (3) subcaudals 64–75 in males and 63–70 in females; (4) skin coloration is black to dark gray, and body coloration is grass green without bands or markings in both sexes; (5) eye color is amber in males and orange-yellow in females; (6) postocular stripe is red and white, extending to the 2nd supralabial in males, but yellow or faintly developed yellow in females; (7) ventrolateral stripe is white (above) and red (below) in males, but yellow in females; (8) temporal scales and occipital scales smooth, dorsal scales rhomboid, feebly keeled except the first row of scales, which are smooth in both sexes.

Morphology of holotype CIB 122871 (Fig. 3). Adult male: body cylindrical and elongated (SVL 457 mm, TAL 110 mm, TL 567 mm); tail relatively long (TAL/TL ratio 0.19). Head triangular, elongated, distinctly separated from neck; head length 24.5 mm (HL/SVL 0.054), head height 8.8 mm, head width 16.3 mm (HW/HL 0.665). Rostral-to-eye distance 8.8 mm bilaterally; eye-to-nostril distance 6.3 mm; interorbital distance 11.2 mm; eye-to-lip distance 3.5 mm; rostral width 3.1 mm. Eyes large (ED 3.0 mm, ED/HL 0.122); vertically elliptical pupil. Distance between the nasal scales 4.04 mm.

Rostral scale clearly visible on dorsal head, about 1/2 internasal scale size. Internasal scales 3, distinctly enlarged; 10 small scales between the supraocular scales. Nasal scale single, undivided, separated from first supralabial, and nostril positioned centrally within the nasal scale. Supralabial 9/8 (second supralabial forms anterior margin of loreal pit, third largest; right third and fourth fused). Infralabial 12/11. Supraocular 1/1. Postnasal 7. A triangular loreal pit is present, bordered by the 2nd supralabial and the middle and lower preocular scales, and positioned closer to the eye than to the nostril. Two small scales lie between the 2nd supralabial and the nasal scale. Preocular 3/3. Postocular 2/2. Suborbital 1/1 (half enters orbit). Ventrals 154. Subcaudals 68. Dorsal scale rows 21-21-15. Anal scale single. Cephalic scales, temporal scales and occipital scales smooth, dorsal scales rhomboid and feebly keeled, except for the first row of scales, which are smooth.

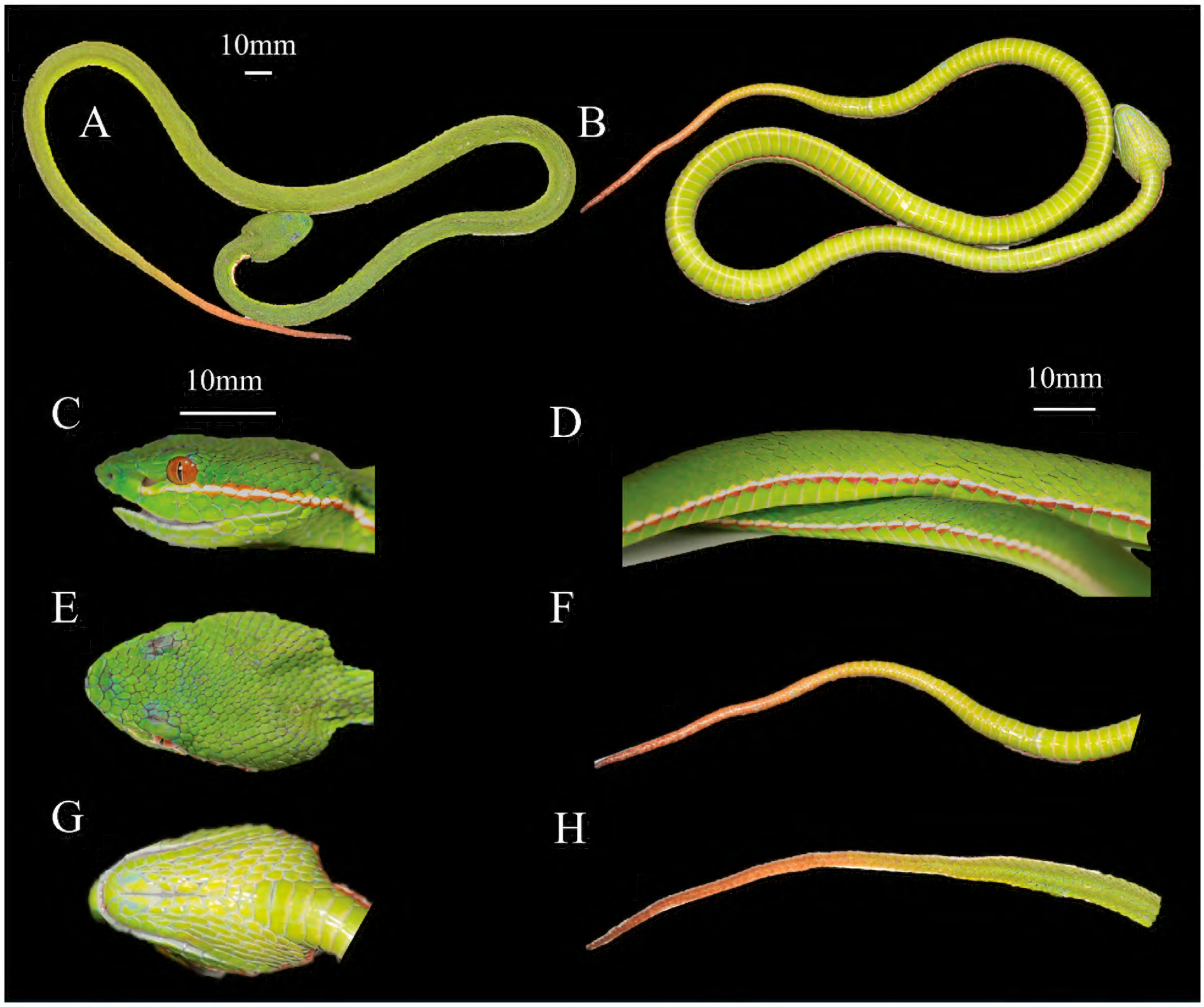

Figure 3. Fresh specimen of the holotype of *Trimeresurus lii* sp. nov. (CIB 122871, adult male). Photographs by Bo Cai.

Coloration in life CIB 122871 (Fig. 3). The skin coloration is bluish-gray. The dorsal scales on the head and body are uniformly grassy green, lacking bands or other markings. The ventral scales are yellow-green. The iris is amber. A distinct white postocular streak originates at the 2nd supralabial. It extends posteriorly, traversing the subocular scale and terminating at the posterior margin of the ultimate supralabial, before continuing onto the neck where it merges with the ventrolateral stripe. The postocular streak forms three distinct layers in the temporal region: red in the upper and lower layers and white in the middle. The ventrolateral stripe runs along the outermost row of dorsal scales onto the tail, where it borders the subcaudal scales on both sides. From the body to the cloacal region, this stripe exhibits a tricolor pattern on the outermost dorsal scales: faint yellow (upper), white (middle), and red (lower). Beyond the cloacal region onto the tail, the yellow fades and disappears, the white gradually diminishes at mid-tail, and the red progressively extends into the distal portions of the subcaudal scales and the caudal scales. The posterior portion of the tail is brown both dorsally and ventrally. The terminus of the tail is dull reddish-brown.

Hemipenial morphology (Fig. 4). The hemipenis from CIB CB2120 extends to the 8th subcaudal scale; the sperm groove bifurcates at the 7th subcaudal scale and follows a Y-shape. The distal portion is differentiated into the calyx region, and the proximal portion into the spine region. The calycozone occupies approximately half the surface area of the acanthozone, with a distinct boundary between the two regions. The calyces are cup-shaped, uniform in morphology and size, with smooth margins. The hemipenial base and the bifurcation point lack spines. Approximately 24 spines of varying sizes are distributed within the acanthozone, with the six basal spines being the largest.

Variation. The species exhibits pronounced sexual dimorphism in coloration from the juvenile stage. Females display a yellow ventrolateral stripe, whereas males exhibit a bicolored pattern with white (above) and red (below). In juveniles: female CIB CB249CD02 bears a yellow postocular streak. Male subadult CIB CB249CD01 has an indistinct postocular streak extending toward the 2nd supralabial. Male juvenile CIB CB249CD03 bears white dorsal spots spaced approximately 5 mm apart (Fig. 5E, F). In adult males, the postocular streak consistently extends to the 2nd supralabial, with variable anterior

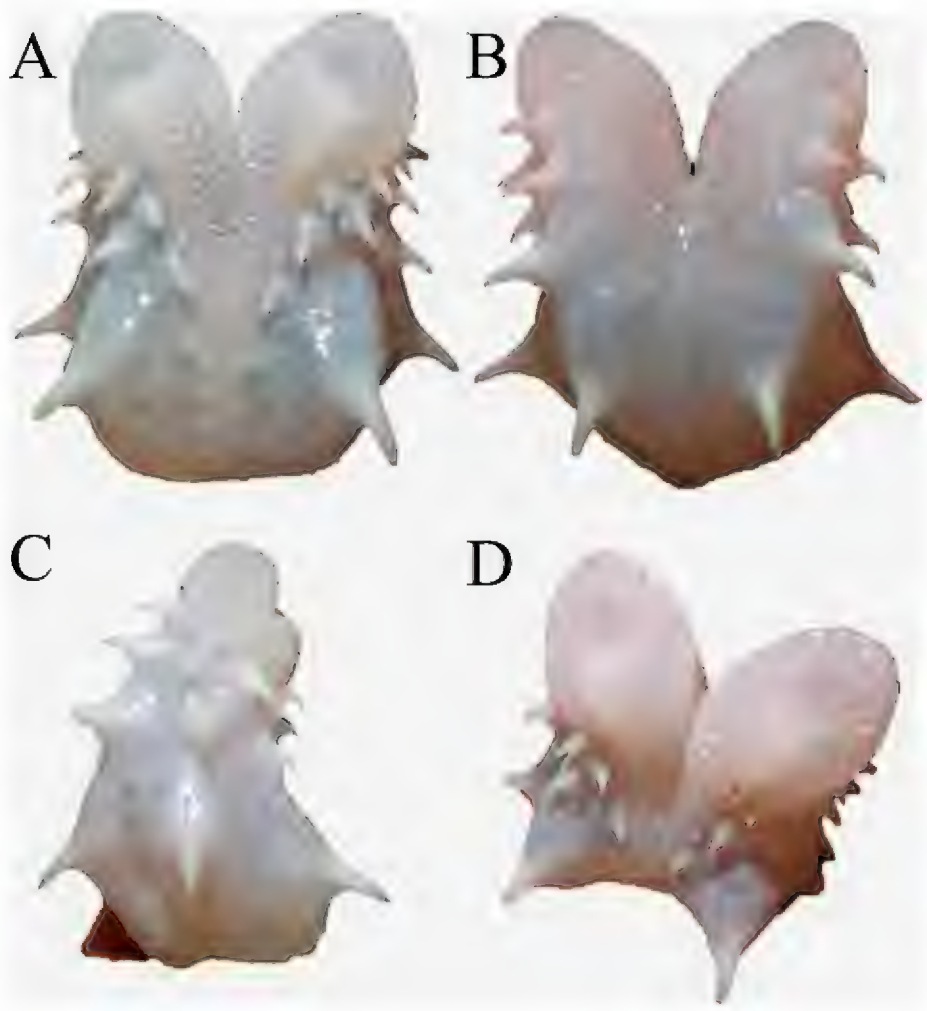

Figure 4. Hemipenis of the paratype of *Trimeresurus lii* sp. nov. (CIB CB2120, adult male). **A.** Anterior view of the sperm groove; **B.** Posterior side of the sperm groove; **C.** Lateral view of the hemipenis; **D.** Distal portion of the hemipenis. Photographs by Bo Cai.

extension: CIB CB2127 reaches the nasal scale. Females retain a faint postocular streak in the head lateral aspect (e.g., holotype CIB 122872).

Comparison. Based on the molecular data, *Trimeresurus lii* sp. nov. is found to be a member of subgenus *Viridovipera*. The species differs from all the known members of *Viridovipera* by the following characters (Table 5).

Trimeresurus lii sp. nov. differs from *T. stejnegeri* by having: (1) higher max SVL in both sexes (675 mm vs. 635 mm [male], 795 mm vs. 670 mm [female]); (2) temporal scales smooth (vs. keeled); (3) occipital scales smooth (vs. keeled); (4) eye color amber (male) and orange-yellow (female) (vs. bright red or amber [male] and yellow or amber [female]); (5) postocular streak extends to the 2nd supralabial, red + white in males (vs. red + white or white, does not extend to the loreal pit); (6) ventrolateral stripe yellow in females (vs. white (above) and red (below) or white or yellow).

Trimeresurus lii sp. nov. differs from *T. loong* by having: (1) higher max SVL in both sexes (675 mm vs. 601 mm [male], 795 mm vs. 657 mm [female]); (2) higher number of ventral scales (152–167 [161.4 ± 4.6] vs. 150–151 [150.3 ± 0.5] in males, 160–168 [163.5 ± 3.3] vs. 157–158 [157.5 ± 0.7] in females); (3) higher SC in females (63–70 [65.3 ± 3.3] vs. 57–64 [60.5 ± 4.9]); MSR 21 (vs. 19); (4) eye color orange-yellow in females (vs. yellowish); (5) postocular streak extends to the 2nd supralabial, red + white in males (vs. thin and white, with a few scale margins slightly tinged with yellow or reddish-brown); (6) ventrolateral stripe yellow in females (vs. absent or white, thin).

Trimeresurus lii sp. nov. differs from *T. truongsonensis* by having: (1) temporal scales smooth (vs. keeled); (2) cephalic scales smooth (vs. keeled); (3) eye color amber (male) and orange-yellow (female) (vs. greenish-yellow in both sexes); (4) postocular streak extends to the 2nd supralabial, red + white in males (vs. absent in both sexes); (5) ventrolateral stripe white (above) and red (below) in males (vs. red + brown, wide); (6) body coloration uniformly grass-green (vs. greenish blue with brown broad bands); (7) higher maximum SVL in both sexes (675 mm

Table 5. Comparative morphological characters among species of the subgenus *Viridovipera*.

Trimeresurus	Sources	KTEM		KCEP		Eye Colour		Postocular Streak	
		♂	♀	♂	♀	♂	♀	♂	♀
***T. lii* sp. nov.**	this study	smooth	smooth	smooth	smooth	amber	orange-yellow	extends to the 2nd supralabial, red + white	yellow or faintly developed
T. loong	Xu et al. 2025a	smooth	smooth	Slightly keeled or smooth	Slightly keeled or smooth	amber, sometimes with a slight reddish hue	Yellowish	thin and white, with a few scale margins slightly tinged with yellow or reddish-brown	Absent
T. nujiang	Liang et al. 2025	slightly keeled	almost smooth	smooth	smooth	golden-yellow	golden-yellow	absent	absent
T. pretiosus	Xu et al. 2025b	slightly keeled	almost smooth	smooth	smooth	reddish-brown	orange-yellow	absent or very faint, thin white	absent
T. yunnanensis	Liang et al. 2025	almost smooth	almost smooth	smooth	smooth	deep red or sepia	golden yellow	red + white	absent (or very faint thin white)
T. mayaae	Rathee et al. 2022; Elangbam et al. 2023; Xu et al. 2025b	almost smooth	almost smooth	smooth	smooth	rusty or greenish	greenish	white or absent	absent
T. medoensis	Zhao et al. 1998; Che et al. 2020; Xu et al. 2025b	slightly keeled	almost smooth	slightly keeled	almost smooth	green or yellowish green	green or yellowish green	absent or faint white	absent
T. stejnegeri	Maki 1931; Zhao et al. 1998; David et al. 2002; Xu et al. 2025a, this study	keeled	keeled	keeled	keeled	bright red or amber (rarely yellow)	yellow or amber	red + white (or white)	absent (or very faint)
T. truongsonensis	Orlov et al. 2004; Xu et al. 2025b	keeled	keeled	keeled	keeled	greenish-yellow	greenish-yellow	absent	absent
T. vogeli	David et al. 2001b; Xu et al. 2025b	smooth	smooth	smooth	smooth	light orange	light orange	absent or faint white	absent

Table 5. Continued.

Trimeresurus	Ventrolateral Stripe		Tail Red	Body Colouration	Max SVL (mm)		VS	
	♂	♀			♂	♀	♂	♀
***T. lii* sp. nov.**	White (above) and red (below)	yellow	yes	uniformly grass-green	675	795	152–167 (161.4 ± 4.6)	160–168 (163.5 ± 3.3)
T. loong	yellow + white + red + brown or thin, white with yellowish margins	absent or white, thin	yes	uniformly grass-green	601	657	150–151 (150.3 ± 0.5)	157–158 (157.5 ± 0.7)
T. nujiang	White (above) and dark red (below)	white, thin	yes	olive drab or uniformly grass-green	694	682	164–173 (168.7 ± 3.6)	165–168 (166.6 ± 1.3)
T. pretiosus	White (above) and dark red (below)	white, thin	yes	uniformly grass-green	516	512	140–143 (141.5 ± 2.1)	142
T. yunnanensis	White (above) and dark red or bright red (below)	white or absent	yes	uniformly grass-green	700	#####	151–168 (161.5 ± 4.4)	155–170 (160.8 ± 5.10)
T. mayaae	White (above) and red (below)	yellowish white	yes	uniformly grass-green	610	590	153–163 (158.1 ± 3.0)	152–153 (152.7 ± 0.6)
T. medoensis	red + white, wide	red + white	yes	uniformly grass-green	553	624	146–151 (148.6 ± 1.8)	145–147 (146.0 ± 1.0)
T. stejnegeri	White (above) and red (below)	white (above) and red (below) or white or yellow	yes	uniformly grass-green	635	670	154–178 (164.5 ± 4.8)	155–173 (163.9 ± 3.5)
T. truongsonensis	red + brown, wide	red + brown	no	greenish blue with brown broad bands	521	488	170–190 (179.8 ± 8.7)	165–167 (166.0 ± 1.0)
T. vogeli	red + white, wide	pale yellow + white, thin	no	uniformly grass-green	661	947	157–169 (162.8 ± 3.7)	157–173 (164.2 ± 5.8)

Table 5. Continued.

Trimeresurus	SC		VS + SC		SC Single or Paired	ASR	MSR	PSR	SL	IL
	♂	♀	♂	♀						
***T. lii* sp. nov.**	64–75 (69.7 ± 4.0)	63–70 (65.3 ± 3.3)	221–238 (231.1 ± 6.3)	223–238 (228.8 ± 6.5)	all paired	21	21	15	9 or 10 (rarely 11)	13-Oct
T. loong	67–68 (67.3 ± 0.5)	57–64 (60.5 ± 4.9)	217–219 (217.5 ± 1.0)	215–221 (218.0 ± 4.2)	all paired	19–23	19	15	10 or 11	11–14
T. nujiang	59–68 (62.8 ± 3.9)	57–60 (58.2 ± 1.1)	226–241 (231.3 ± 6.9)	222–226 (224.8 ± 1.8)	partly single	19–21 (rarely 22)	19	15	9 or 10	13-Nov
T. pretiosus	56–58 (57.0 ± 1.4)	54	198–199 (198.5 ± 0.7)	196	partly single	19	19	15	8 or 9	10 or 11
T. yunnanensis	59–71 (66.5 ± 3.9)	53–64 (57.4 ± 3.1)	221–235 (228.7 ± 4.7)	209–232 (218.1 ± 7.0)	all paired	19–21	19–21	15	11-Sep	13-Oct
T. mayaae	54–69 (61.1 ± 4.5)	53–55 (54.0 ± 1.0)	211–231 (218.9 ± 6.1)	205–208 (206.7 ± 1.5)	all paired	19–28	19 or 21	15–17	8–10	13-Oct
T. medoensis	55–59 (57.0 ± 1.4)	58–60 (59.0 ± 1.0)	201–208 (205.6 ± 2.9)	204–206 (205.0 ± 1.0)	all paired	17 (rarely 19)	17	13 (rarely	8 or 9	10-Aug
T. stejnegeri	60–80 (70.3 ± 4.2)	58–70 (63.4 ± 2.9)	218–256 (234.9 ± 7.7)	218–237 (227.5 ± 4.5)	all paired	21–25	21 or 23	15	12-Sep	14-Oct
T. truongsonensis	65–71 (67.4 ± 2.5)	61–70 (66.7 ± 4.9)	235–259 (247.2 ± 10.7)	228–235 (232.7 ± 4.0)	all paired	21	21	15	11-Sep	13-Nov
T. vogeli	63–71 (67.0 ± 2.3)	59–70 (63.0 ± 3.8)	221–238 (229.8 ± 4.9)	218–238 (227.7 ± 6.3)	all paired	21-23	21 (rarely 20)	15	11-Sep	16-Nov

vs. 521 mm in males, 795 mm vs. 488 mm in females); (8) lower number of ventral scales in males (152–167 vs. 170–190); (9) tail red (vs. not red).

Trimeresurus lii sp. nov. differs from *T. vogeli* by having: (1) eye color amber (male) and orange-yellow (female) (vs. light orange in both sexes); (2) postocular streak extends to the 2nd supralabial, red + white in males (vs. absent or faint white and does not extends to the loreal pit); (3) ventrolateral stripe yellow in females (vs. pale yellow + white, thin in females); (4) lower maximum SVL in females (795 mm vs. 947 mm); (5) tail red (vs. not red).

Trimeresurus lii sp. nov. differs from *T. yunnanensis* by having: (1) eye color amber (male) and orange-yellow (female) (vs. deep red or sepia in males, golden yellow in females); (2) postocular streak extends to the 2nd supralabial, red + white in males (vs. not extending to the loreal pit); (3) lower maximum SVL in both sexes (675 mm vs. 700 mm in males, 795 mm vs. 1047 mm in females); (4) ventrolateral stripe yellow in females (vs. white or absent); (5) higher number of subcaudal scales in females (63–70 vs. 53–64); (6) higher number of MSR (21 vs. 19–21).

Trimeresurus lii sp. nov. differs from *T. mayaae* by having: (1) eye color amber (male) and orange-yellow (female) (vs. rusty or greenish in males, greenish in females); (2) postocular streak extends to the 2nd supralabial, red + white in males (vs. white and not extending to the loreal pit or absent); (3) higher maximum SVL in both sexes (675 mm vs. 610 mm in males, 795 mm vs.

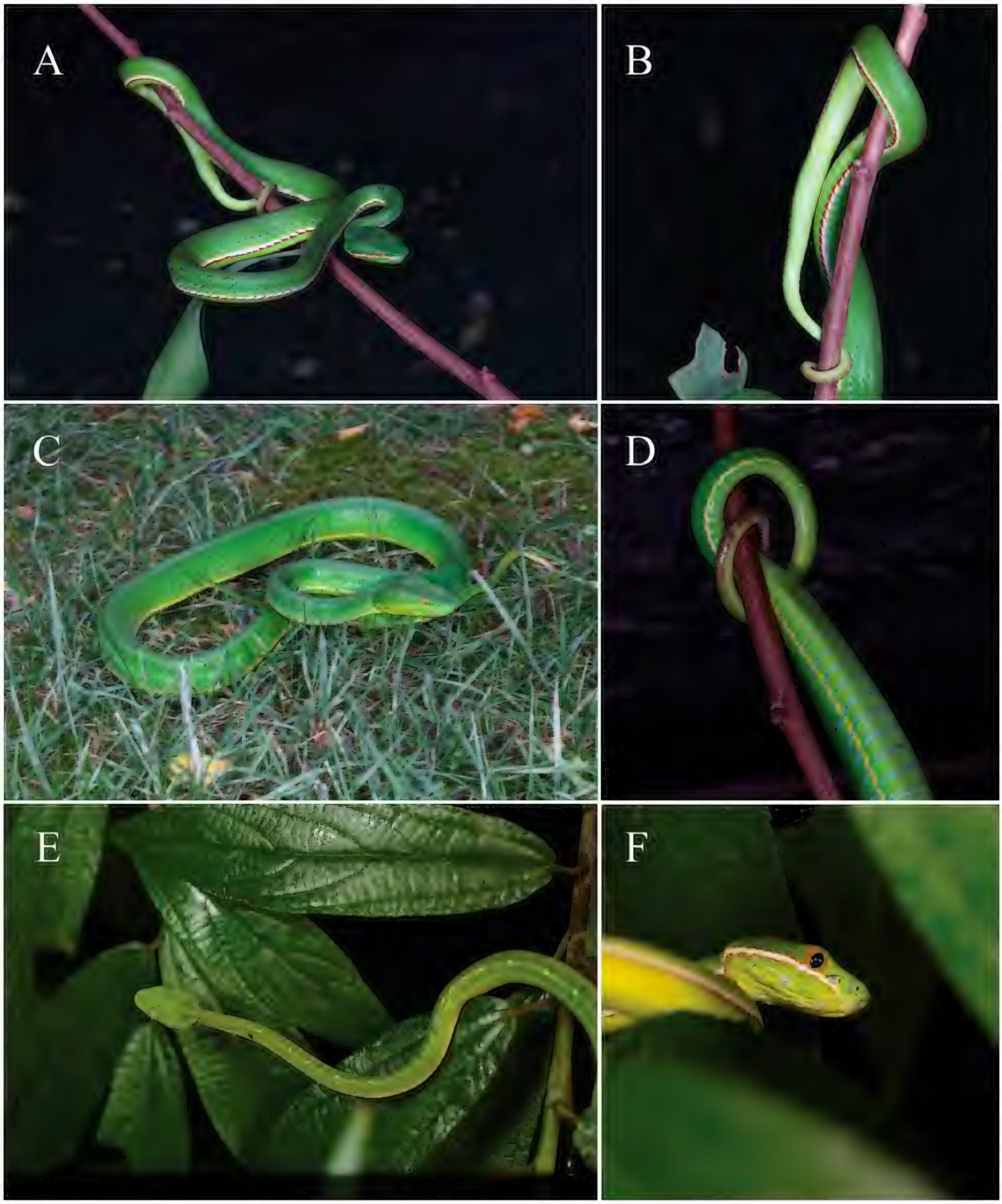

Figure 5. *Trimeresurus lii* sp. nov. in life: paratype CIB CB2120, male (**A**, **B**); allotype CIB 122872, female (**C**, **D**); and paratype CIB CB249CD03, juvenile male (**E, F**). Photographs by Bo Cai.

590 mm in females); (4) higher number of ventral scales in females (160–168 vs. 152–153); (5) higher number of subcaudal scales in both sexes (64–75 vs. 54–69 in males, 63–70 vs. 53–55 in females).

Trimeresurus lii sp. nov. differs from *T. medoensis* by having: (1) eye color amber (male) and orange-yellow (female) (vs. green or yellowish green in both sexes); (2) postocular streak extends to the 2nd supralabial, red + white in males (vs. absent or faint white and extends to the loreal pit); (3) higher maximum SVL in both sexes (675 mm vs. 553 mm in males, 795 mm vs. 624 mm in females); (4) higher number of ventral scales in both sexes (152–167 vs. 146–151 in males, 160–168 vs. 145–147 in females); (5) higher number of subcaudal scales in both sexes (64–75 vs. 55–59 in males, 63–70 vs. 58–60 in females); (6) higher number of ASR and MSR scales (21 vs. 17 in both sexes).

Trimeresurus lii sp. nov. differs from *T. nujiang* by having: (1) eye color amber (male) and orange-yellow (female) (vs. golden-yellow in both sexes); (2) postocular streak extends to the 2nd supralabial, red + white in males (vs. absent); (3) lower number of ventral scales in males (152–167 vs. 164–173); (4) higher number of subcaudal scales in males (64–75 vs. 59–68) and higher in females (63–70 vs. 57–60); (5) higher number of MSR scales (21 vs. 19 in both sexes); (6) SC all paired (vs. partly single).

Trimeresurus lii sp. nov. differs from *T. pretiosus* by having: (1) postocular streak extends to the 2nd supralabial, red + white in males (vs. absent or very faint, thin white and not extending to the loreal pit); (2) higher maximum SVL in both sexes (675 mm vs. 516 mm in males, 795 mm vs. 512 mm in females); (3) higher number of ventral scales in both sexes (152–167 vs. 140–143 in males, 160–168 vs. 150–158 in females); (4) higher number of subcaudal scales in both sexes (64–75 vs. 56–68 in males, 63–70 vs. 54 in females); (5) SC all paired (vs. partly single); (6) higher number of MSR scales (21 vs. 19 in both sexes).

Natural history and distribution

Trimeresurus lii sp. nov. is currently confirmed from several sites in Sichuan Province, including Xiling Snow Mountain within the Chengdu sector of the Giant Panda National Park, Yuping Mountain in Hongya County, and Emei Mountain in Emeishan City. Photographs further indicate a possible occurrence in Qingchuan County (Guo et al. 2021) and in Longcanggou National Forest Park in Yingjing County (personal communication with Haolong Fang). It occupies elevations of approximately 1,100–1,500 m a.s.l., all within the West China Rain Zone, one of the major precipitation centers in the region (Hu et al. 2023) (Fig. 1).

Across these montane areas, individuals are typically found in the transitional zone between evergreen and deciduous broad-leaved forests. They utilize bamboo stands, shrub–grass layers, and rocky streamside microhabitats, often resting 2–5 m above ground level (Fig. 6). The surrounding herpetofauna includes: *Odorrana ichangensis* Chen, 2020, *O. margaretae* (Liu, 1950), *Quasipaa boulengeri* (Günther, 1889), *Rana omeimontis* Ye & Fei, 1993, *Boulenophrys omeimontis* (Liu, 1950), *Amolops chaochin* Jiang, Ren, Lyu & Li, 2021, *Diploderma szechwanensis* (Hu & Zhao, 1966), *Ovophis makazayazaya* (Takahashi, 1922), *Protobothrops jerdonii* (Günther, 1875), *P. mucrosquamatus* (Cantor, 1839), *Ptyas major* (Günther, 1858), *Pareas chinensis* (Barbour, 1912), *P. boulengeri* (Angel, 1920), and *Rhabdophis chiwen* Chen, Ding, Chen & Piao, 2020. Observations are most frequent from July to September. Although occasional daytime activity occurs, the species is primarily nocturnal. After several days of rainfall followed by clear weather, individuals may emerge to bask.

Reproductive information is still limited, but based on our observations, one temporarily captive female gave birth to eight offspring in mid-August, confirming that the species is ovoviviparous.

Clinical manifestations and management of envenomation

Gang Wang was bitten by a male *Trimeresurus lii* sp. nov. from Mt. Emei (approximately 600 mm in total length) on the ring finger of his right hand at 22:15 on 9 September 2021 (Fig. 7). The bite produced a single puncture wound with immediate bleeding. Within 10 minutes, swelling rapidly progressed from the finger to the entire hand, accompanied by severe aching, stabbing pain, and numbness of the affected finger. By the time he arrived at Leshan People's Hospital at 00:01 on 10 September 2021, swelling had extended to the elbow. Hematological examination revealed difficulty in venipuncture (initially unsuccessful from dorsal veins and successful from the femoral vein), hypotension, and mild dizziness. Wang received polyvalent antivenom (commercially labeled for *Agkistrodon halys* and *Agkistrodon acutus*), along with anti-inflammatory medications. After discharge at 05:00 on the same day, he experienced transient dizziness and mild nausea and vomiting, which resolved within 20 minutes. Edema gradually decreased, with swelling at the elbow resolving by 14 September 2021

Figure 6. Habitat of *Trimeresurus lii* sp. nov.: **A.** Landscape of the habitat; **B.** Microhabitat. Photographs by Bo Cai.

Figure 7. Clinical manifestations of envenomation and treatment. **A.** Swelling began on the ring finger 11 minutes after the bite (22:26, 9 September 2021); **B.** The entire right hand was swollen 13 minutes after the bite, accompanied by severe pain (22:28, 9 September 2021); **C, D.** Approximately 2 days after antivenom administration, the hand remained swollen with no sign of reduction, and swelling extended above the elbow (22:50, 11 September 2021); **E.** Swelling began to subside approximately 3 days after antivenom administration (22:50, 12 September 2021); **F.** Swelling in the elbow region had nearly resolved, and only mild hand swelling remained approximately 5 days after antivenom administration (19:35, 14 September 2021). Photographs by Gang Wang.

and full recovery achieved by 18 September 2021. Notably, G.W. subjectively noted a marked decline in immune function during the following year.

Discussion

While comprehensive nuclear genomic analyses would undoubtedly refine assessments of lineage independence (Toews and Brelsford 2012), practical constraints currently limit such approaches in *Trimeresurus* systematics. Public repositories contain scarce nuclear sequence data for the subgenus *Viridovipera* and related taxa, and tissue availability from rare, recently collected specimens—particularly those critical to initial species descriptions—remains severely limited. Consequently, our integrative methodology, which combines mitochondrial phylogenetics with diagnostic morphological characters, aligns with established taxonomic protocols for this genus (Idiiatullina et al. 2023, 2024a, b, c; Mirza et al. 2023; Liang et al. 2025; Pawangkhanant et al. 2025; Xu et al. 2025a, b). We emphasize that future investigations into the phylogeography and evolutionary dynamics of this rapidly radiating lineage must prioritize expanded genomic sampling, especially nuclear markers, to resolve complex patterns of diversification and historical gene flow.

The discovery of *Trimeresurus lii* sp. nov. transcends taxonomic novelty, offering pivotal insights into the evolutionary history and biogeographic structuring of the subgenus *Viridovipera*. Phylogenetic analyses reveal its exclusive sister relationship with *T. loong*, which together define a previously unrecognized clade endemic to the eastern Hengduan Mountains. This finding elucidates a tripartite biogeographic pattern within *Viridovipera*: (1) the *T. medoensis* group (*T. medoensis*, *T. mayaae*, and *T. pretiosus*), confined to regions south of the Himalayas; (2) the *T. stejnegeri* group (*T. nujiang*, *T. stejnegeri*, *T. truongsonensis*, *T. vogeli*, and *T. yunnanensis*), spanning the Hengduan Mountains to eastern China and Southeast Asia, with its distribution shaped by the complex topography of the Yunnan–Guizhou Plateau and the riverine barriers of the Mekong and Salween systems; and (3) the newly identified *T. lii*–*T. loong* lineage, restricted entirely to the isolated montane ecosystems of the eastern Hengduan Mountains—a previously poorly recognized center of endemism isolated by the valleys of the Jinsha River system.

The discovery of *Trimeresurus lii* sp. nov. within the Sichuan Giant Panda National Park underscores a critical yet underappreciated dimension of conservation in this flagship reserve: its dual role as both a refuge for charismatic megafauna and a cradle of cryptic herpetofaunal diversity. While the park's conservation mandate has historically focused on giant pandas and their bamboo forest habitats, our findings

demonstrate that its complex topography and climatic heterogeneity harbor numerous undocumented lineages with extremely limited distributions. *T. lii* sp. nov. is currently known only from the West China Rain Zone. Historical records of *T. stejnegeri* from Wen County in Gansu Province and adjacent areas lack adequate morphological documentation and clear imagery (Wang 1991; Yao and Gong 2012), making it impossible to determine whether these represent *T. lii*. The taxonomic status of these populations therefore requires further investigation through dedicated fieldwork and molecular studies. Our study incorporated *Trimeresurus* sequences from the southern and eastern Sichuan Basin previously analyzed by Guo et al. (2016). These specimens either clustered with *T. stejnegeri* sequences from the type locality or represented *T. sichuanensis*. Morphological re-evaluation of historical of specimens identified as *T. stejnegeri* from western Sichuan in Zhao et al. (1998) revealed consistent morphological mismatches with the type series from Fujian Province; rather, these historical specimens align precisely with the diagnostic characters of *T. lii* sp. nov., including smooth cephalic scales and the distinctive male postocular streak extension pattern (Table 2). Field surveys across the entire elevational range of the species (1,100–1,500 m a.s.l.) confirmed no sympatric occurrence with other *Trimeresurus* species, establishing *T. lii* as a true regional endemic. This new species provides a compelling case for expanding conservation priorities to include narrow-range endemic whose presence signals ecosystem integrity. The persistence of such narrow endemics amid accelerating habitat fragmentation highlights the urgent need for fine-scale habitat connectivity planning—particularly along elevational gradients—where climate-driven range shifts will increasingly challenge species survival.

The restricted range of *Trimeresurus lii* sp. nov. further highlights the West China Rain Zone as an irreplaceable evolutionary theater. Here, relict plant assemblages and cryptic vertebrate radiations converge under a dynamic, climate-mediated selective regime, a synergy that demands targeted conservation attention. Future studies incorporating genomic-scale data, ecological niche modeling, and paleoclimatic reconstructions will be essential to determine whether *T. lii* sp. nov. represents a relictual survivor of ancient montane forests or a product of recent adaptive radiation—a distinction with profound implications for predicting biodiversity responses to anthropogenic climate change in this vulnerable region. Until such resources become available, the formal description of morphologically and genetically diagnosable lineages such as *T. lii* sp. nov. provides the essential taxonomic foundation upon which conservation prioritization and evolutionary research must rest.

Acknowledgments

We sincerely thank Professor Jiatang Li for his invaluable encouragement and guidance throughout this study. We are grateful to Professor Peng Guo of Yibin University for his assistance with species identification. We also extend our appreciation to Mr. Xu Yuhao for his contributions to morphological data collection, species identification, and manuscript revision. Special thanks go to Professor Biao Yang from West China Normal University and Mr. Doudou Chen, a Master's graduate from Xiamen University, for their support. Finally, we acknowledge the logistical and administrative support provided by the Sichuan Provincial Administration of the Giant Panda National Park and the Natural Resources Bureau of Emeishan City during our fieldwork. This research was funded by the National Natural Science Foundation of China (NSFC32270494 and NSFC-JSPS32411540022) and the Special Survey Project on Amphibians and Reptiles in the Chengdu Section of Giant Panda National Park (2025014).

References

Ao JM, David P, Bordoloi S, Ohler A (2004) Notes on a collection of snakes from Nagaland, northeast India, with 19 new records for this state. Russian Journal of Herpetology 11(2): 155–162.

Bu CF, Zheng XC, Zhao XT, Xu TY, Bai X, Jia YK, Chen ML, Hao LL, Xiao JF, Zhang Z, Zhao WM, Tang BX, Bao YM (2024) GenBase: A Nucleotide Sequence Database. Genomics, Proteomics & Bioinformatics 22(3): qzae047. https://doi.org/10.1093/gpbjnl/qzae047

Burbrink FT, Lawson R, Slowinski JB (2000) Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): A critique of the subspecies concept. Evolution 54(6): 2107–2118. https://doi.org/10.1554/0014-3820(2000)054[2107:MDPOTP]2.0.CO;2

Cai B (2023) A field guide to the reptiles of Sichuan. Science Press, Beijing, China, 145 pp. [In Chinese]

Cai B (2025) Class Reptilia in Catalogue of Life China: 2025 Annual Checklist in Species 2000 China Node. http://www.sp2000.org.cn/browse/browse_taxa [accessed on 20 May 2025]

Captain A, Deepak V, Pandit R, Bhatt B, Athreya R (2019) A new species of pitviper (Serpentes, Viperidae, *Trimeresurus* Lacépède, 1804) from West Kameng District, Arunachal Pradesh, India. Russian Journal of Herpetology 26(2): 111–122. https://doi.org/10.30906/1026-2296-2019-26-2-111-122

Che J, Jiang K, Yan F, Zhang YP (2020) Amphibians and Reptiles in Tibet: Diversity and Evolution. Science Press, Beijing, China, 800 pp. [in Chinese]

Chen ZN, Zhang L, Shi JS, Tang YZ, Guo YH, Song ZB, Ding L (2019) A new species of the genus *Trimeresurus* from Southwest China (Squamata, Viperidae). Asian Herpetological Research 10(1): 13–23. https://doi.org/10.16373/j.cnki.ahr.180062

Chen ZN, Yu JP, Vogel G, Shi SC, Song ZB, Tang YZ, Yang J, Ding L, Chen CS (2020) A new pit viper of the genus *Trimeresurus* (Lacépède, 1804) (Squamata, Viperidae) from Southwest China. Zootaxa 4768: 112–128. https://doi.org/10.11646/zootaxa.4768.1.7

CNCB-NGDC Members and Partners (2025) Database Resources of the National Genomics Data Center, China National Center for Bioinfomation in 2025. Nucleic Acids Research 53(D1): D30–D44.

Creer S, Malhotra A, Thorpe RS (2003) Assessing the phylogenetic utility of four mitochondrial genes and a nuclear intron in the Asian pit viper genus *Trimeresurus*: separate, simultaneous, and conditional

data combination analyses. Molecular Biology and Evolution 20(8): 1240–1251. https://doi.org/10.1093/molbev/msg136

David P, Captain A, Bhatt B (2001a) On the occurrence of *Trimeresurus medoensis* Djao in Djao & Jiang, 1977 (Serpentes: Viperidae: Crotalinae) in India, with a redescription of this species and notes on its biology. Hamadryad 26(2): 222–238.

David P, Vidal N, Pauwels OSG (2001b) A morphological study of Stejneger's pitviper *Trimeresurus stejnegeri* (Serpentes, Viperidae, Crotalinae), with the description of a new species from Thailand. Russian Journal of Herpetology 8(3): 205–222. https://doi.org/10.30906/1026-2296-2019-8-%s-205-222

David P, Vogel G, Pauwels OSG, Vidal N (2002) Description of a new species of the genus *Trimeresurus* from Thailand, related to *Trimeresurus stejnegeri* Schmidt, 1925 (Serpentes, Crotalidae). The Natural History Journal of Chulalongkorn University 2: 5–19. https://doi.org/10.58837/tnh.2.1.102858

David P, Mathew R (2005) Notes on some noteworthy snake specimens deposited in the collections of Eastern Regional Station of the Zoological Survey of India. Records of the Zoological Survey of India 104(3–4): 83–90. https://doi.org/10.26515/rzsi/v104/i3-4/2005/159303

David P, Vogel G, Dubois A (2011) On the need to follow rigorously the Rules of the Code for the subsequent designation of a nucleospecies (type species) for a nominal genus which lacked one: The case of the nominal genus *Trimeresurus* Lacépède, 1804 (Reptilia, Squamata, Viperidae). Zootaxa 2992(1): 1–51. https://doi.org/10.11646/zootaxa.2992.1.1

Dawson K, Malhotra A, Thorpe RS, Guo P, Mrinalini, Ziegler T (2008) Mitochondrial DNA analysis reveals a new member of the Asian pitviper genus *Viridovipera* (Serpentes, Viperidae, Crotalinae). Molecular Phylogenetics and Evolution 49(1): 356–361. https://doi.org/10.1016/j.ympev.2008.05.044

Elangbam PS, Biakzuala L, Shinde P, Decemson HT, Vabeiryureilai M, Lalremsanga HT (2023) Addition of four new records of pitvipers (Squmata, Crotalinae) to Manipur, India. Journal of Threatened Taxa 15(6): 23315–23326. https://doi.org/10.11609/jott.8486.15.6.23315-23326

Guo P, Wang YZ (2011) A new genus and species of cryptic Asian green pitviper (Serpentes, Viperidae, Crotalinae) from southwest China. Zootaxa 2918(1): 1–14. https://doi.org/10.11646/zootaxa.2918.1.1

Guo P, Liu Q, Zhong G, Zhu F, Yan F, Tang T, Xiao R, Fang M, Wang P, Fu X (2015) Cryptic diversity of green pitvipers in Yunnan, South west China (Squamata, Viperidae). Amphibia-Reptilia 36(3): 265–276. https://doi.org/10.1163/15685381-00003004

Guo P, Liu Q, Zhu F, Zhong GH, Chen X, Myers EA, Che J, Zhang L, Ziegler T, Nguyen TQ, Burbrink FT (2016) Complex longitudinal diversification across South China and Vietnam in Stejneger's pit viper, *Viridovipera stejnegeri* (Schmidt, 1925) (Reptilia, Serpentes, Viperidae). Molecular Ecology 25: 2920–2936. https://doi.org/10.1111/mec.13658

Guo P, Liu Q, Wu Y, Zhu F, Zhong G (2021) Pitvipers of China. Science Press, Beijing, China, 249pp.

Hu W, Qiao X, Chen K, Tang Y (2023) Geographic extent of the West China Rain Zone determined by precipitation characteristics. Mountain Research 41: 662–675. [In Chinese] https://doi.org/10.16089/j.cnki.1008-2786.000778

Idiiatullina SS, Pawangkhanant P, Tawan T, Worranuch T, Dechochai B, Suwannapoom C, Nguyen TV, Chanhome L, Poyarkov NA (2023) Limestone jewel: A new colourful karst-dwelling pitviper (Serpentes, Viperidae, *Trimeresurus*) from the poorly explored borderlands of southern Peninsular Thailand. Vertebrate Zoology 73: 697–716. https://doi.org/10.3897/vz.73.e109854

Idiiatullina SS, Nguyen TV, Bragin AM, Pawangkhanant P, Le DX, Vogel G, David P, Poyarkov NA (2024a) A new species of green pitviper of the *Trimeresurus macrops* complex (Reptilia, Serpentes, Viperidae) from South Central Coast Region of Vietnam. Zootaxa 5474(4): 375–411. https://doi.org/10.11646/zootaxa.5474.4.2

Idiiatullina SS, Nguyen TV, Pawangkhanant P, Suwannapoom C, Chanhome L, Mirza ZA, David P, Vogel G, Poyarkov NA (2024b) An intgrative taxonomic revision of the *Trimeresurus popeiorum* species complex (Reptilia, Serpentes, Viperidae), with descriptions of two new species from the Indo-Burma biodiversity hotspot. Vertebrate Zoology 74: 303–342. https://doi.org/10.3897/vz.74.e113347

Idiiatullina SS, Pawangkhanant P, Suwannapoom C, Tawan T, Chanhome L, Nguyen TV, David P, Vogel G, Poyarkov NA (2024c) Another new species of karst-associated pitviper (Serpentes, Viperidae, *Trimeresurus*) from the Isthmus of Kra, Peninsular Thailand. European Journal of Taxonomy 930: 20–52. https://doi.org/10.5852/ejt.2024.930.2489

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Phylogenetics and Evolution 30: 772–780. https://doi.org/10.1093/molbev/mst010

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution 35: 1547–1549. https://doi.org/10.1093/molbev/msy096

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2017) PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. Molecular Biology and Evolution 34: 772–773. https://doi.org/10.1093/molbev/msw260

Li JN, Liang D, Wang YY, Guo P, Huang S, Zhang P (2020) A large scale systematic framework of Chinese snakes based on a unified multilocus marker system. Molecular Phylogenetics and Evolution 148: 106807. https://doi.org/10.1016/j.ympev.2020.106807

Liang YT, Ding L, Vogel G, Chen ZN, Wu ZJ (2025) A new species of the genus *Trimeresurus* Lacépède, 1804 (Reptilia, Squamata, Viperidae) from southwestern China. Zoosystematics and Evolution 101(4): 1653–1668. https://doi.org/10.3897/zse.101.162424

Maki M (1931) A monograph of the snakes in Japan. Dai Ichi Shobo, Tokyo, Japan, 1–7 + 1–240, Errata; (1), (1), 1–3 + 1–57, Pl. 1–39. [In English/Japanese] [The separate Japanese text volume and Pl. 40–86 appeared in 1933]

Malhotra A, Thorpe RS (2000) A phylogeny of the *Trimeresurus* group of pit vipers: New evidence from a mitochondrial gene tree. Molecular Phylogenetics and Evolution 16(2): 199–211. https://doi.org/10.1006/mpev.2000.0779

Malhotra A, Thorpe RS (2004a) A phylogeny of four mitochondrial gene regions suggests a revised taxonomy for Asian pitvipers (*Trimeresurus* and *Ovophis*). Molecular Phylogenetics and Evolution 32: 83–100. https://doi.org/10.1016/j.ympev.2004.02.008

Malhotra A, Thorpe RS (2004b) Maximizing information in systematic revisions: a combined molecular and morphological analysis of a cryptic green pitviper complex (*Trimeresurus stejnegeri*). Biological Journal of the Linnean Society 82(2): 219–235. https://doi.org/10.1111/j.1095-8312.2004.00354.x

Mirza ZA, Lalremsanga HT, Bhosale H, Gowande G, Patel H, Idiiatullina SS, Poyarkov NA (2023) Systematics of *Trimeresurus popeiorum* Smith, 1937 with a revised molecular phylogeny of Asian pitvipers of the genus *Trimeresurus* Lacépède, 1804 sensu lato. Evolutionary Systematics 7(1): 91–104. https://doi.org/10.3897/evolsyst.7.97026

Nguyen LT, Schmidt HA, Haeseler AV, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Molecular Biology and Evolution 32(1): 268–274. https://doi.org/10.1093/molbev/msu300

Orlov NL, Ryabov SA, Bui TN, Ho CT (2004) A new species of *Trimeresurus* (Ophidia, Viperidae, Crotalinae) from the karst region in central Vietnam. Russian Journal of Herpetology 11(2): 139–149.

Parkinson CL, Zamudio KR, Greene HW (2000) Phylogeography of the pitviper clade *Agkistrodon*: historical ecology, species status, and conservation of cantils. Molecular Ecology 9(4): 411–420. https://doi.org/10.1046/J.1365-294X.2000.00854.X

Pawangkhanant P, Idiiatullina SS, Nguyen TV, Ruangsuwan T, Matsukoji T, David P, Suwannapoom C, Poyarkov NA (2025) A snake can change its finery: A new cryptic species of the *Trimeresurus kanburiensis* complex (Reptilia, Serpentes, Viperidae) from Central Thailand with an unusual ontogenetic color change. Zootaxa 5621(5): 514–546. https://doi.org/10.11646/zootaxa.5621.5.2

Pope CH (1935) The reptiles of China. Turtles, crocodilians, snakes, lizards. Natural History of Central Asia, Vol. 10. American Museum of Natural History, New York, USA, 604 pp. https://doi.org/10.5962/bhl.title.12104

Rathee YS, Purkayastha J, Lalremsanga HT, Dalal S, Biakzuala L, Muansanga L, Mirza ZA (2022) A new cryptic species of green pitviper of the genus *Trimeresurus* Lacépède, 1804 (Serpentes, Viperidae) from northeast India. PLoS ONE 17: e0268402. https://doi.org/10.1371/journal.pone.0268402

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Sanders KL, Malhotra A, Thorpe RS (2006) Combining molecular, morphological and ecological data to infer species boundaries in a cryptic tropical pitviper. Biological Journal of the Linnean Society. Linnean Society of London 87(3): 343–364. https://doi.org/10.1111/j.1095-8312.2006.00568.x

Schmidt KP (1925) New reptiles and a new salamander from China. American Museum Novitates 157: 1–5.

Schmidt KP (1927) Notes on Chinese reptiles. Bulletin of the American Museum of Natural History 54(6): 467–551.

Skwor T (2012) The use of DNASTAR lasergene educational software with molecular techniques to support bacterial identification. Tested Studies for Laboratory Teaching Proceedings of the Association for Biology Laboratory Education 33: 327–334.

Toews DPL, Brelsford A (2012) The biogeography of mitochondrial and nuclear discordance in animals. Molecular Ecology 21: 3907–3930. https://doi.org/10.1111/j.1365-294X.2012.05664.x

Uetz P, Freed P, Aguilar R, Reyes F, Hošek J (2025) The Reptile Database. http://www.reptiledatabase.org [accessed on 30 September 2025]

Wang XT (1991) Vertebrate Fauna of Gansu. Gansu Science and Technology Press, Lanzhou, China, 276–277.

Xu YH, Deng J, Zhang T, Nguyen TV, Weng S, Poyarkov NA, Vogel G, Sun F, Liao C, Peng F (2025a) A 'little dragon' from Kunming City: A new green pit viper from Yunnan Province, China (Squamata, Viperidae, *Trimeresurus*). Zoosystematics and Evolution 101(4): 2267–2293.

Xu YH, Nguyen TV, Wang ZQ, Zhang TR, Poyarkov NA, Wei C, Vogel G, Li JC, Deng JD, Sun FY, Peng LF, Weng SY (2025b) A new green pitviper of the genus *Trimeresurus* Lacépède, 1804 (Squamata, Viperidae) from Xizang, China. Animals 15: 2675. https://doi.org/10.3390/ani15182675

Yao CY, Gong DJ (2012) Amphibiansand Reptiles of Gansu. Gansu Science and Technology Press, Lanzhou, China, 153–154.

Zhang D, Gao FL, Jakovlić I, Zou H, Zhang J, Li WX, Wang GT (2020) PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. Molecular Ecology Resources 20(1): 348–355. https://doi.org/10.1111/1755-0998.13096

Zhao EM (2003) Coloured Atlas of Retiles of Sichuan. China Forestry Publishing House, Beijing, China, 292 pp. [in Chinese]

Zhao EM (2006) Snakes of China. Vol. I. Anhui Science and Technology Publishing House, Hefei, China, 372 pp. [in Chinese]

Zhao EM, Huang MH, Zong Y (1998) Fauna Sinica: Reptilia. Vol. 3. Squamata, Serpentes. Science Press, Beijing, China, 522 pp. [in Chinese]